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RESEARCH ARTICLE

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Functional diversity of Collembola is reduced in soils subjected to short-term, but not long-term, geothermal warming

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Abstract

1. Human activities have caused global changes of atmospheric chemistry resulting in increased temperature especially in the colder regions of the northern hemisphere. Since warming of the environment can have drastic effects on terrestrial ecosystems it is important to experimentally evaluate the extent of such effects in long-term field-based experiments. In this study we make use of both recent (short-term) and long-term geothermal warming of Icelandic soils to examine the responses of Collembola, an ecologically important group of soil invertebrates, to warming.
2. On the basis of metabolic scaling theory, we hypothesized that species of small size would be more successful in warmed soils than species of larger size. Further we expected that top-soil-dwelling species would benefit more from warming than deep-soil-dwelling species. In order to test these hypotheses we sampled Collembola along replicated gradients of increasing temperature in areas that had been heated for about 6 years and more than 50 years respectively. Collembola were identified to species level, counted and the community-weighted mean trait scores for six functional and ecological traits were calculated.
3. Results show that both short-term and long-term soil warming caused a shift towards a higher relative abundance of species with small body size. Furthermore, abundance of top-soil-dwelling Collembola tended to increase after short-term warming, but the opposite was observed after long-term warming.
4. Using trait-based diversity indices (FRic and RaoQ), we show that functional richness and diversity of Collembola communities was significantly reduced (almost halved) as a result of short-term soil warming to about 10°C above normal, but this effect was not detected in plots equally warmed for more than 50 years. This indicates that the functional diversity of Collembola communities have high resilience towards soil warming in a long-term perspective.

KEYWORDS
adaptation, ecological traits, global warming, soil ecology, springtails

1 | INTRODUCTION

The activities of humans have caused global changes of atmospheric chemistry and climate. These changes are likely to continue in the near future due to projected increasing concentrations of greenhouse gases in the atmosphere, resulting in increased temperatures over large parts of the Earth's surface and, especially, in the colder regions of the northern hemisphere (IPCC, 2013). Physiological reaction rates are dependent on temperature, which is therefore probably the most important environmental factor determining the abilities of ectothermic animals to move, feed, grow and reproduce (Willmer, Stone, & Johnston, 2000). In addition, extremely high and low temperatures are damaging, and the thermal tolerance of species often sets the limits for the geographical distribution of populations (Berman, Meshcheryakova, Alfimov, & Leirkh, 2002; Huey & Kingsolver, 1989; Kellermann et al., 2012). Environmental change such as warming of a habitat may result in physiological constraints of individuals, which will have impact on fitness and ultimately cause changes in community composition of the particular habitat (Sinclair et al., 2016). Global warming can be considered as a gradually increasing or cumulative selection pressure on the ecosystem with a chronic effect on the species present in the community. Some species may be pre-adapted to warming or may be able to adapt through evolutionary processes. If the adaptive potential of the species in the community is of sufficient magnitude the ecological resilience of the community may be sufficient to absorb the disturbance and return to the original state (Bengtsson, 2002; Holling, 1973).

Since increasing temperatures can have drastic effects on terrestrial communities (Parmesan & Yohe, 2003; Walther et al., 2002), it is important to experimentally evaluate the extent of such effects. Several field-based experiments that manipulate climatic parameters have addressed this problem, but most of these studies are short-term (<5–10 years) and very few have been running for more than a decade (Blankinship, Niklaus, & Hungate, 2011; Bokhorst et al., 2012; Estiarte et al., 2016; Holmstrup et al., 2013). Although such (relatively) short-term experiments give us insight into the immediate responses of organisms to warming effects, adjustments of community and ecosystem composition to a warmer environment may require many generations of different species to reach a new equilibrium state, requiring observations at a longer time-scale than used in most manipulation studies. One way to assess the long-term impact of warming on terrestrial communities is the use of natural geothermal temperature gradients within local areas establishing "outdoor laboratories" (O'Gorman et al., 2014). Although geothermal warming does not influence the temperature of the above-ground atmosphere to any great extent (Sigurdsson et al., 2016), such systems may be used to test hypotheses about the influence of warming *per se* on soil organisms. In this study, we make use of both recent (short-term) and long-term geothermal warming of Icelandic soils to examine the responses of soil invertebrates to both recent and long-term warming.

We aimed to study the effect of soil warming on springtails (Collembola), an important group of soil microarthropods that enhances the decomposition of dead plant material in ecosystems (Hopkin, 1997). Microarthropods positively affect the decomposition of leaf and root litter directly via litter consumption and indirectly via an increase in the rate of microbial activity due to fragmentation of plant litter, microbial propagulae dispersal and grazing on decomposer fungi and bacteria (Cragg & Bardgett, 2001; Seastedt, 1984; Tiunov & Scheu 2005). We used recently (6 years at time of sampling) emerged gradients in soil temperature, caused by an earthquake in May 2008 that induced local shifts in geothermal systems, thereby heating previously unwarmed grassland areas in south-west Iceland. In these areas, and in similar nearby grassland areas that had been heated for more than 50 years (also due to geothermal heating), we compared the Collembola communities along soil temperature gradients ranging from unwarmed soils to soils warmed by *c.* 10°C (Sigurdsson et al., 2016). This allowed us to compare short-term and long-term responses of Collembola communities to soil warming. As a supplement to traditional taxonomic evaluation of the community we also employed an analysis of community-weighted mean traits, since species responses to warming are likely linked to their physiological and ecological attributes. Such analysis allows an alternative grouping of species' responses which may generate new and more mechanistic explanations of community changes than the traditional taxonomic approach (McGill, Enquist, Weiher, & Westoby, 2006). Species traits play a central role, because they determine not only how a species responds to environmental change, but also how these responses may influence ecosystem functions. Morphological, ecophysiological or ecological traits have previously been used to explain responses of Collembola to climatic manipulations (Bokhorst et al., 2012; Makkonen et al., 2011).

Collembola like other soil organisms often exhibit a distinct vertical stratification (Berg, Kniese, Bedaux, and Verhoef, 1998; Hopkin, 1997; Lee, 1985) and are often divided into surface-dwelling litter species (epigeic species), and truly soil-living species which occupy deeper soil layers (eu-edaphic species). Hemi-edaphic species occupy the upper soil layers and deeper litter and have an intermediate vertical distribution. Thermal variability in soil is highly influenced by the depth; for example diurnal temperature amplitude could be >15°C at 5 cm depth, and <5°C at 15 cm depth in a Danish grass field during summer (Holmstrup, 1999). Variability in the thermal conditions of a particular habitat is often reflected in the thermal plasticity of the species living there. Eu-edaphic species occupy relatively stable environments, whereas hemi-edaphic and especially epigeic species can be exposed to more fluctuating and more extreme thermal environments. Accordingly, eu-edaphic species of Collembola have been shown to have relatively poor acclimation responses to changes in temperature and are less able to cope with rapid shifts to extreme high or low temperatures compared to epigeic and hemi-edaphic species (Bahrndorff, Loeschcke, Pertoldi, Beier, & Holmstrup, 2009; Van Dooremalen, Berg, & Ellers, 2013).

Van Straalen (1994) has shown that developmental rate of eggs of epigeic and hemi-edaphic species was faster and more responsive to

increasing temperature than in eu-edaphic species, which would give an ecological advantage to the species living in and on the surface layers if temperatures increase, and a better ability to exploit short periods of warming (Berg et al., 2010; Van Straalen, 1994). Our main hypothesis was therefore that epigeic and hemi-edaphic Collembola would be more tolerant to high temperatures and generally benefit more than eu-edaphic Collembola from increased mean temperatures and increased fluctuations in temperature. Furthermore, we hypothesized that the functional diversity of Collembola communities of the recently warmed site would be lowered more by warming than in the communities of the long-term warmed site, where species composition of the communities would have been adjusted to warming.

2 | MATERIALS AND METHODS

2.1 | Field site

The study was conducted at the ForHot research site (Sigurdsson et al., 2016), which is located in the Hengill geothermal area, 40 km east of Reykjavik, Iceland (64°00′01″N, 21°11′09″W; 100–225 m a.s.l.). The dominant soil type in this area is Brown Andosol. The mean annual temperature between 2004 and 2014 in the nearby village Eyrarbakki was 5.2°C, and the mean temperature of the warmest and coldest months, July and December, were 12.2°C and −0.1°C respectively. The mean annual precipitation during the same period was 1431 mm (Icelandic Meteorological Office). The main vegetation type at the ForHot research site was unmanaged grassland, dominated by *Agrostris capillaris*, *Ranunculus acris* and *Equisetum pratense*. In this grassland, two areas that had been subjected to geothermal warming for different periods of time were studied. One area had probably been warmed for centuries, based on different historical sources and soil profile surveys, and no change in the location of the hotspots had been recorded during the preceding 50 years (Sigurdsson et al., 2016). This grassland was termed "LWG" ("Long-term Warming Grassland"). The second grassland, which was located 2 km *SE* from LWG, had been warmed since 29 May 2008, when a large earthquake shifted geothermal systems to previously unwarmed soils (Sigurdsson et al., 2016). This study area was termed "SWG" ("Short-term Warming Grassland"). Within these sites different heat sources (so-called "hotspots") were located. At site SWG there were two, and a site LWG four hotspots (e.g. see in Figure S1).

Soil warming in the study plots was caused by heat conduction from the underlying bedrock that was warmed from within by hot groundwater. The soil warming increment was relatively constant throughout the year as soil temperature at 10 cm depth (T_s) changed to similar degree, with seasonal fluctuations of T_s at all warming levels. Extreme deviations were exceptional (Sigurdsson et al., 2016). Temperatures increased with depth (below 10 cm) at the warmer ends of the transects (i.e. at +5 and +10°C), but temperature differences between 10 and 5 cm depth were always <2°C (Sigurdsson et al., 2016). Geothermal water was confined within the bedrock and no signs of soil contamination by geothermal byproducts were found. No large changes in pH or soil moisture occurred along the warming gradients (Sigurdsson et al., 2016). Species richness of plants was higher in the LWG than in SWG plots (Michielsen, 2014). Interestingly, no significant changes in dominant plant species occurred along the soil warming gradients, however, the length of growing season linearly extended with on average 2.1 days per °C soil warming (Leblans et al., 2017).

2.2 | Experimental design

An overview of the study area is shown in Figure 1. In October 2012, five replicate transects radiating from the hotspots were established in each site. In the LWG site, four transects (transect 1–4) were placed relatively close to each other covering an area of *c*. 50 × 100 m, and transect 5 was placed about 500 m away (Figure 1). At the SWG site, transects 1–3 covered an area of about 40 × 40 m about 500 m from transects 4–5 that covered an area of about 50 × 30 m (Figure 1). At each transect, we selected five T_s levels including unwarmed soil and four (three at LWG) warming levels of *c*. +0.5, +2 (only at SWG), +3.5 and +8°C. At each T_s level, a 2 × 2 m permanent measurement plot was established, accompanied with a 0.5 × 0.5 m subplot for destructive measurements in which the soil cores for microarthropods were taken. The transects at each site thus represented five similar temperature gradients running either uphill or downhill from the heat sources providing a certain natural randomization. The length of each transect was typically *c*. 50 m and the distance between permanent plots typically got shorter with increasing temperatures, but not less than *c*. 5 m. Due to the physical conditions at the study sites (e.g. local steep slopes, large boulders/rocks, and unequal physical distance between isotherms [e.g. see in Figure S1]), it was not always possible to place plots and transects, respectively, with equal distance between them (Figure 1). Thus, the design provided replication of the warming and warming duration as far as the natural physical conditions allowed. Due to the small body size and relatively low mobility of Collembola (Bengtsson, Hedlund, & Rundgren, 1994), we judge the field plots to be sufficiently large to avoid noteworthy emi- or immigration and edge effects from neighbouring plots of different temperature.

2.3 | Temperature measurements

Plot-specific T_s was recorded with HOBO TidbiT v2 Water Temperature Data Loggers (Onset Computer Corporation, USA) on an hourly basis at 10 cm soil depth from 8 May 2013 until sampling of microarthropods (11 September 2014). The plot-specific temperature data allowed us to use regressions in the analysis of Collembola data (see section 2.6). For this purpose, we calculated overall mean temperature (mean of all hourly measurements during the period), absolute maximum, absolute minimum, overall temperature amplitude and mean diurnal temperature amplitude.

The establishment of plots along the soil temperature gradients resulted in soils with increasing mean temperature, but also

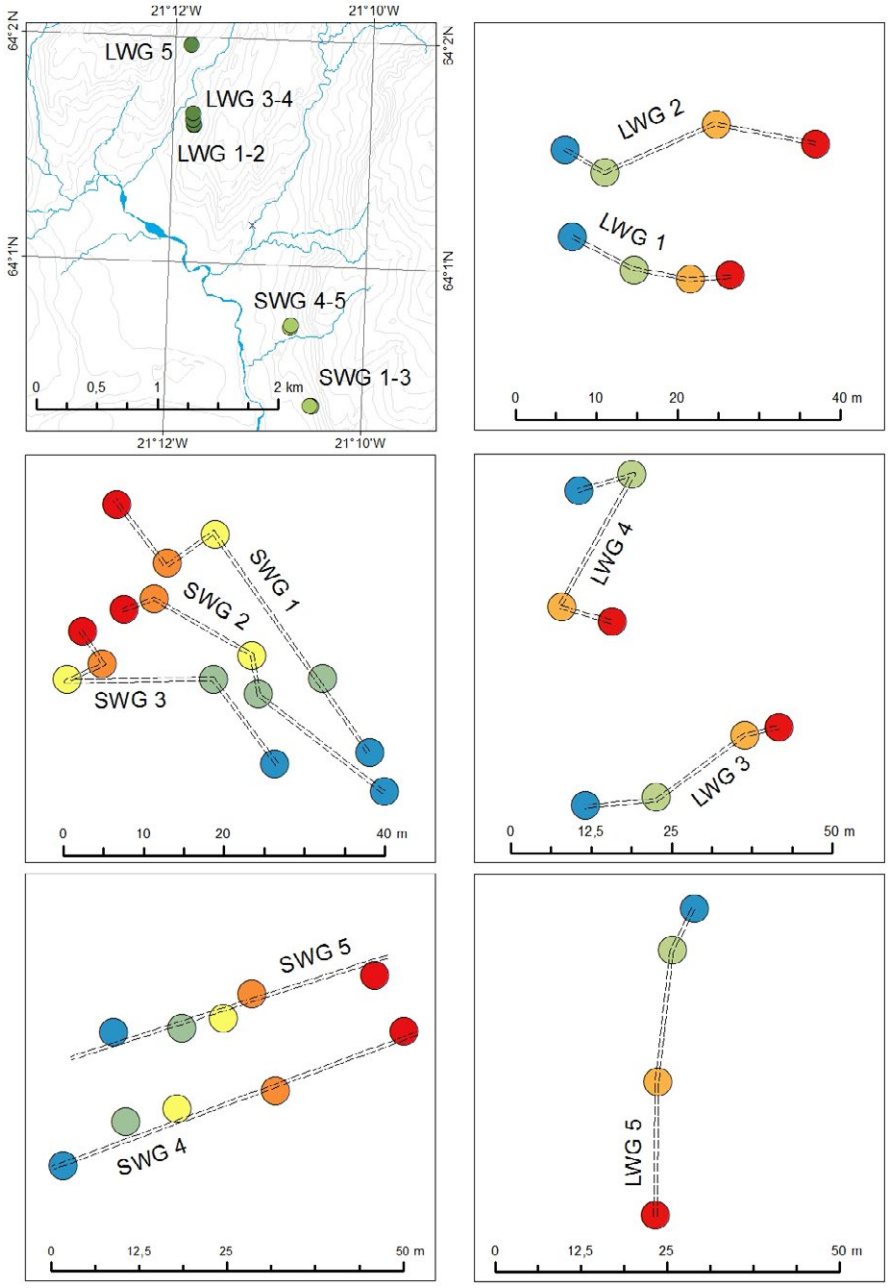

FIGURE 1 Overview of the ForHot study sites at Reykir, southern Iceland. Geothermal transects warmed since May 2008 were termed "short-term warming grassland" (SWG) and transects warmed for at least 50 years were termed "long-term warming grassland" (LWG). Each transect included five (SWG) or four (LWG) permanent study plots where mean annual soil temperature was unaltered (blue circles) or warmed by *c.* 0.5°C (green circles), +2 (yellow circles), +3.5 (orange circles) and +8°C (red circles). Map made by S. H. Brink

with different variability in soil temperature. The general trend was that variability in soil temperature increased with increasing soil warming (pairwise correlations mean temperature vs. absolute (annual) temperature amplitude: SWG: $r = .55$, $p = .0037$; LWG: $r = .56$, $p = .0002$; and mean temperature vs. mean diurnal temperature amplitude: SWG: $r = .55$, $p = .004$; LWG: $r = .4$, $p = .01$; Figures S2 and S3). Thus, both the absolute amplitude of temperatures and the mean diurnal temperature amplitude increased with mean temperature, but mostly so in SWG (Figures S2 and S3). In addition, mean diurnal temperature amplitude and absolute temperature amplitude were highly positively correlated with each other (pairwise correlations absolute temperature amplitude vs. diurnal temperature amplitude: SWG: $r = .92$, $p < .0001$, LWG: $r = .73$, $p < .0001$). Therefore, we used only mean soil temperature as explanatory variable in the further analysis of Collembola data.

2.4 | Sampling of Collembola

Microarthropods were sampled on 11 September 2014 using a cylindrical soil corer with an inner diameter of 6 cm to a depth of 5 cm. Two soil cores were sampled from each plot. The samples were kept in closed plastic cylinders at 5°C until extraction which was initiated within 5 days after collection. Microarthropods were extracted in a high gradient extraction apparatus (MacFadyen type), where the temperature in the upper compartment increased stepwise from 25°C to 50°C within 7 days while the temperature at the lower compartment remained constant at 3°C (Krogh & Pedersen, 1997). If the

TABLE 1 Description of functional traits and ecological preferences used in the analysis

Trait	Data type	Attribute
Life-form	Ordinal	1 = epigeic 2 = hemi-edaphic 3 = eu-edaphic
Body mass	Quantitative	in µg
Dispersal ability	Ordinal	1 = low dispersal ability 2 = high dispersal ability
Food preference	Ordinal	1 = chewing mouthparts 2 = scratching mouthparts 3 = piercing mouthparts
Moisture preference	Ordinal	1 = xerophilic 2 = xero-mesophilic 3 = mesophilic 4 = meso-hygrophilic 5 = hygrophilic
Habitat width	Ordinal	1 = stenotopic 2 = eurytopic

soil cores had not dried after 7 days, the extraction was continued until dryness was attained. The microarthropods were collected in benzoic acid and subsequently conserved and stored in glycerol until identification. Collembola were identified to species level according to Fjellberg (1998, 2007). The two subsamples from each plot were combined and abundance per m^2 was calculated.

2.5 | Collembola traits

We selected six functional traits and ecological preferences that expectedly would be responsive to warming (outlined in Table 1). For simplicity, we refer to all the species characteristics listed in Table 1 as "traits" although this is an extension of the definition of traits used by Violle et al. (2007). These traits included life-form, moisture preference, habitat width, dispersal ability, food preference and body mass. Life-form relates to the adaptation of Collembola to life in soil (Hopkin, 1997) and was based on a set of five morphological traits, i.e. body pigmentation, furca length, number of ommatidia, hair length and length of antenna relative to body size (see da Silva, Berg, Serrano, Dubs, and Sousa (2012) for details) and resembles the vertical stratification grouping of Gisin (1943). Since "life-form" is a combined trait, we used Principal Component Analysis to separate species and group them into one of three groups: eu-edaphic, hemi-edaphic or epigeic (Figure S4). Collembola life-form is a highly responsive trait in relation to abiotic stressors. From surface to soil-dwelling species, there is a reduction in body pigmentation, furca length, number of ommatidia, hair length and relative length of antenna. These changes pin-point into the direction of adaptation to life in soil and are proxies for physiological traits (heat and cold tolerance; drought and inundation tolerance) that we did not have for all these species. Therefore, we used these morphological proxies to define vertical stratification groups. Soil-dwelling species tend to be more sensitive to climate fluctuations, have a reduced metabolic rate and an increase in parthenogenetic mode of reproduction. We therefore argue that this group should respond strongly to warming compared to surface-living species. Species with an epigeic life-form are colourful (often with contrasting stripes or spots), have eight ocelli on each side of the head, long antenna, a fully developed furca and are often large in size. Eu-edaphic species on the other hand are often blind, without cuticular pigmentation, have short antenna and a reduced or absent furca. The hemi-edaphic species are intermediate in these traits (diffuse coloration, 1–7 ocelli, furca reduced, antenna of intermediate size). Values for these morphological traits were taken from Fjellberg (1998, 2007). Moisture preference was based on occurrence of species in habitats differing in soil moisture and was used as a proxy for drought tolerance. Species were classified into moisture preference groups following Kuznetsova (2003). If the hygro-preference of a species was not mentioned in this publication, Fjellberg (1998, 2007) and the identification series Synopsis on Palaearctic Collembola (Dunger, 1994) were consulted. To harmonize the moisture preference information across publications we used Kuznetsova (2003) for calibration. Habitat width is a proxy for environmental tolerance (Lindberg & Bengtsson, 2005). Species were classified as either eurytopic or stenotopic based on Kuznetsova (2002), and the same procedure was used for missing species as described in moisture preference. Dispersal ability was based on a combination of three morphological traits related to the mobility of the species, i.e. the number of ocelli, furca development and relative leg length, following Ponge, Dubs, Gillet, Sousa, and Lavelle (2006). Species with good eye sight (eight ommatidia), relatively long legs and a well-developed furca were classified as strong dispersers, whereas poor dispersers have shorter legs, a reduced furca and fewer ommatidia. Collembola diet is correlated with mouth part structure (Hopkin, 1997), making mouthpart morphology a good proxy for food preference. Information on mouthpart structure was taken from Fjellberg (1998, 2007). Finally, body dry mass was indirectly estimated from body length, using dry weight to body length regressions provided by Caballero, Baquero, Arino, and Jordana (2004). Maximum body length for each species was taken from Fjellberg (1998, 2007) and used to calculate body dry mass selecting the allometric length–weight relationships from Caballero et al. (2004) of a species that was similar in body form to our species. The values of the six traits are shown for all species in Table S1.

To determine if temperature had an influence on these traits we computed community-weighted mean trait values (T_m) for each experimental plot as:

$$T_m = \sum_i p_i x_i,$$

where x is the trait value of the i-th species and p_i is the relative abundance of the i-th species in a sample.

2.6 | Statistical analysis

We analysed soil warming effects on species richness and abundance of hemi-edaphic, and eu-edaphic species using linear mixed effects models. Epigeic species occurred in very low abundance and were therefore not analysed as a group. Abundance of species was ln

transformed prior to analysis to meet assumptions for linear models (normally distributed errors, homogeneity of error variances). These variables were analysed for the effects of Site (LWG or SWG; i.e. warming duration), Temperature and the interaction between those. We specified Site, Temperature, and their interaction as fixed effects and transects (nested within site) as random effect. Transects effects were included to account for the fact that observations within a transect will tend to be more correlated due to their spatial proximity. All models were fitted using the function lmer in the statistical R package LME4 (Bates, Machler, Bolker, & Walker, 2015), and the significance of the effects of each model component was obtained by likelihood ratio tests. We tested for an interaction effect by comparing the full model containing the interaction (Site × Temperature) effect with a reduced model where the interaction effect was omitted. We also analysed each site separately and tested for an effect of temperature by backward model reduction. Here the full model [temperature plus transect (random)] was tested against a reduced model only containing transect. Residual plots were inspected visually to examine for violation of homoscedasticity.

We analysed for each site the effect of temperature on the community-weighted mean of the traits: life-form, moisture preference, habitat width, dispersal ability, food preference and body mass. With the exception of body mass, these ordinal traits were re-coded into numeric values assuming equi-distance between subsequent categories. We used linear mixed models, treating temperature as a fixed effect, and transect as random effect. Significance of temperature was obtained by backward model reduction as described above. Prior to analysis, to meet model assumptions, body mass was ln transformed, and habitat width square root transformed. No transformation was applied to the remaining variables.

To study if the trait divergence of species changed with soil warming, we calculated for each plot in each transect two indices of functional diversity: The functional richness index (FRic) and Rao's quadratic entropy index of diversity (RaoQ) (Pavoine & Bonsall, 2011; Villeger, Mason, & Mouillot, 2008). These indices were calculated using the five ordinal ecological species traits (see Table 1). FRic reflects the range of trait variability in the trait space using the convex hull approach. RaoQ expresses the sum of dissimilarities in the trait space among all possible pairs of species weighted by the product of relative species abundance in a sample. We computed these indices using the FD package for R (Laliberte & Legendre, 2010). For each site we analysed for the effect of temperature using the same linear model as for community-weighted trait means.

Site (SWG and LWG; duration of soil warming) was not replicated in a completely randomized test design (Figure 1). Within SWG there were two, and within LWG four hotspots (or heat sources) from which the transects were radiating. Analysing diversity data with models using "Hotspot" as random factor nested within Site, for replication of warming duration is thus a potentially more conservative test for the effect of temperature than when using the models described above that use transects as random factor. The results of these analyses yielded virtually identical results (Table S2) and are not reported further. In addition, a similar analysis of diversity data using mean diurnal temperature amplitude as fixed factor also led to the same overall conclusion (Table S3) and is not reported further.

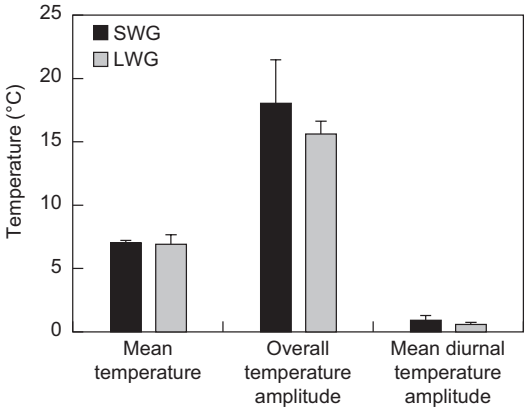

FIGURE 2 Mean temperature, mean overall temperature amplitude (i.e. seasonal variability) and mean diurnal temperature amplitude of unwarmed control plots at short-term warming grassland (SWG) and long-term warming grassland (LWG). Values are shown as $M \pm SE$ ($N = 5$). Control plots of SWG and LWG do not differ significantly in their thermal characteristics (Student *t*-tests, NS). Temperature parameters are based on hourly measurements at 10 cm depth during the period from 8 May 2013 until sampling of microarthropods (11 September 2014)

3 | RESULTS

3.1 | Abundance and species richness

Continuous measurements of T_s showed that the soil thermal conditions in control plots (i.e. unwarmed plots) at SWG and LWG were essentially equal (Figure 2). Also the Collembola communities of unwarmed control plots at SWG and LWG were similar for species richness, abundance and community-weighted mean traits (Table 2). In the control plots at both sites, the Collembola communities were dominated by the same 4–5 eu-edaphic and hemi-edaphic species (Table 2), but in total 22 species were found (Table S1). Epigeic species were rare and occurred only in low abundance in our samples probably because our sampling method was not adapted to epigeic Collembola (epigeic species may simply escape during sampling of soil cores).

Species richness varied among sites ($\chi^2 = 5.03$, $df = 1$, $p = .025$) and decreased with temperature ($\chi^2 = 11.4$, $df = 1$, $p = .0007$; Figure 3). Overall, including all temperatures, the species richness was highest at LWG. On average and at both SWG and LWG, the species number per sample decreased from 8.6 at control temperature (mean temperature 7°C) to about seven species per sample at 16°C (Figure 3). Moreover, we did not detect any significant Site × Temperature interaction suggesting that the impact of soil warming on species richness was similar in both sites (Site × Temperature interaction: $\chi^2 = 2.29$, $df = 1$, $p = .13$). The abundance of hemi-edaphic species showed, however, a significant interaction effect between Site and Temperature (Site × Temperature interaction: $\chi^2 = 8.28$, $df = 1$, $p = .0004$; Figure 4). The abundance

TABLE 2 Description of the Collembola community in control plots at short-term warming grassland (SWG) and long-term warming grassland (LWG) (i.e. unwarmed plots at both sites). The table shows the abundances (individuals per m^2) of dominant species and groups, species richness and selected community-weighted traits. All values are *M* ± *SE* (*N* = 5). Except for abundance of *Folsomia quadrioculata* there are no significant differences between sites. More information on the functional traits and ecological preferences are shown in Table 1

Species/groups/traits	SWG *M* ± *SE*	LWG *M* ± *SE*
Folsomia manolachei^H	23687 ± 12513	22273 ± 2249
Protaphorura pseudovanderdrifti^E	13929 ± 3235	17430 ± 5002
Parisotoma notabilis^H	6258 ± 2220	7778 ± 3668
Isotomiella minor^E	5338 ± 1434	8591 ± 1625
Pseudanurophorus binoculatus^E	2864 ± 2440	2015 ± 1429
Tullbergiinae spp^E	1697 ± 950	1874 ± 672
Folsomia quadrioculata^H	177 ± 177	3712 ± 981
Megalothorax minimus^E	1520 ± 329	848 ± 351
Friesea truncata^H	318 ± 240	530 ± 274
Eu-edaphic Collembola	25526 ± 6160	30970 ± 5223
Hemi-edaphic Collembola	30511 ± 14399	34647 ± 5276
Epigeic Collembola	71 ± 71	0 ± 0
Total Collembola	56107 ± 18004	65617 ± 9251
Species richness	8.6 ± 0.5	8.8 ± 0.4
Life-form	2.50 ± 0.08	2.47 ± 0.04
Body mass (μg)	10.63 ± 1.65	11.73 ± 1.55
Moisture preference	3.85 ± 0.06	3.94 ± 0.08
Habitat width	1.71 ± 0.07	1.75 ± 0.04
Dispersal ability	1.01 ± 0.00	1.01 ± 0.00
Food preference	1.01 ± 0.01	1.01 ± 0.01

^{H}*hemi-edaphic*; ^{E}*eu-edaphic*.

of hemi-edaphic species increased significantly with temperature at the SWG site (effect of Temperature at SWG: $\chi^2 = 4.84$, $df = 1$, $p = .028$) and decreased significantly with temperature at the LWG site (effect of Temperature at LWG: $\chi^2 = 6.1$, $df = 1$, $p = .014$). It should be noted, however, that the positive effect of temperature in SWG was driven by one sample of extraordinarily high abundance (160,000 individuals per m^2 at 19°C), and re-running the analysis without this value removed the significant positive effect of temperature at SWG ($\chi^2 = 1.29$, $df = 1$, $p = .26$), whereas there was still a significant Site × Temperature interaction ($\chi^2 = 4.36$, $df = 1$, $p = .037$). For eu-edaphic species we detected no interaction between Site and Temperature (Site × Temperature interaction, eu-edaphic Collembola: $\chi^2 = 0.17$, $df = 1$, $p = .68$). Abundance of eu-edaphic Collembola varied among sites (effect of Site: $\chi^2 = 6.86$, $df = 1$, $p = .01$), and showed a marginally significant decrease with increasing temperature (effect of Temperature: $\chi^2 = 3.68$, $df = 1$, $p = .055$). Overall, including all temperatures, the abundance of eu-edaphic Collembola was highest at LWG (data not shown).

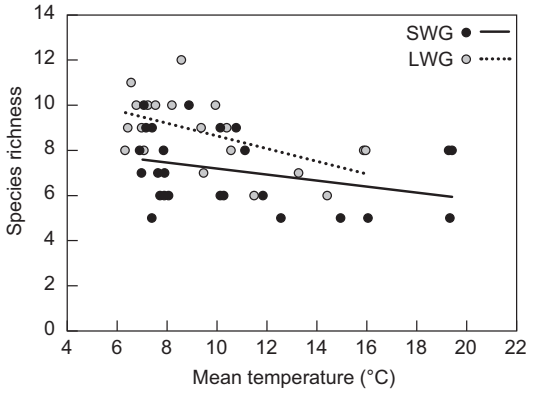

FIGURE 3 Species richness of Collembola at the short-term warming grassland (SWG) and long-term warming grassland (LWG) sites in relation to mean soil temperature. Soil warming had a significant negative effect on species richness at both sites. Lines show the slopes of the linear mixed model. Mean temperature is based on hourly measurements at 10 cm depth during the period from 8 May 2013 until sampling of microarthropods (11 September 2014)

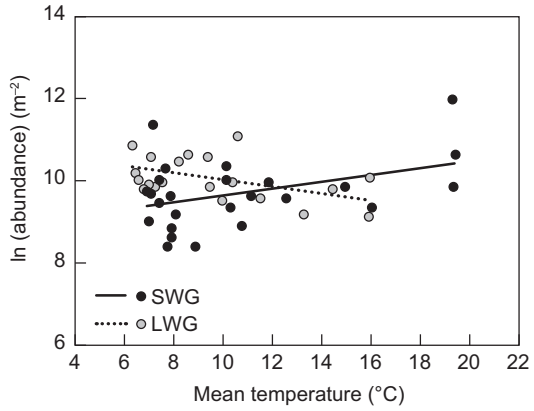

FIGURE 4 Abundance of hemi-edaphic Collembola at the short-term warming grassland (SWG) and long-term warming grassland (LWG) sites in relation to mean soil temperature. Soil warming had a significant positive effect on abundance at SWG, but a negative effect at LWG. Lines show the slopes of the linear mixed model. Mean temperature is based on hourly measurements at 10 cm depth during the period from 8 May 2013 until sampling of microarthropods (11 September 2014)

3.2 | Community traits

Life-form (the community-weighted mean trait value) was negatively influenced by warming at SWG, but not at LWG, where no significant change in life-form was seen (Table 3; Figure 5). This means that the community at SWG became less dominated by eu-edaphic species (or more dominated by hemi-edaphic species) with increasing T_s. Community-weighted mean body mass was significantly reduced by mean temperature at both sites (Table 3; Figure 6).

Community-weighted mean habitat width was significantly influenced by temperature at SWG, but not at LWG (Table 3; Figure 7). At SWG, the proportion of eurytopic species increased with

TABLE 3 Summary of statistics for selected community-weighted mean traits and two indices of functional diversity (FRic and RaoQ) at the short-term warming grassland (SWG) and long-term warming grassland (LWG) sites. Significant effects are shown in bold. More information on the ecological traits can be found in Table 1

		SWG		LWG	
Parameter	**Source variable**	χ^2	***p*-value**	χ^2	***p*-value**
Life-form	Mean temperature	60.5	**<.001**	0.13	.71
Body mass	Mean temperature	14.43	**.00015**	7.77	**.005**
Habitat width	Mean temperature	11.32	**.0008**	1.25	.26
Moisture preference	Mean temperature	3.67	.056	1.54	.21
Dispersal ability	Mean temperature	2.6	.10	1.43	.23
Food preference	Mean temperature	0.0001	.99	0.00011	.99
FRic	Mean temperature	13.62	**<.001**	1.08	.30
RaoQ	Mean temperature	22.86	**<.001**	1.77	.18

temperature, and these were completely dominating the community at the highest temperatures. The community-weighted mean moisture preference was not influenced by soil temperature and nor was dispersal ability (Table 3). The Collembola communities were strongly dominated by mesophilic and meso-hygrophilic species with low dispersal ability (Table 2). Most of the species found in our study had chewing mouth parts and the food preference trait was not influenced by soil temperature (Table 3).

Functional richness was negatively influenced by soil temperature in SWG, but not in LWG (Figure 8; Table 3). Likewise, RaoQ was negatively influenced by soil temperature in SWG, but not in LWG (Figure 8; Table 3).

4 | DISCUSSION

The main result of our study is that functional diversity of Collembola was drastically impaired by soil warming in the short term, but not in the long term. To the best of our knowledge, our experiment is the first to assess and compare soil warming effects on soil animal communities in both the short-term and long-term perspective. This comparison is important because climate change is taking place at a slow pace (over decades or centuries rather than annual), which will give species and ecosystems time to respond, evolve and perhaps adapt. Thus, the inherent problem with manipulation experiments that aim to elucidate the consequences of climate change is that they often last only for a limited period of time [see review in (Blankinship et al., 2011)], with the exception of a handful of studies lasting more than a decade (Estiarte et al., 2016; Holmstrup et al., 2013; Makkonen et al., 2011). A valuable aspect of the present experiment is that there were little – if any – differences in the control communities of these two situations giving a good opportunity to compare short-term and long-term responses of Collembola to soil warming.

Dispersal ability, as a community-weighted mean trait, was not influenced by soil warming in our study, meaning that we found no shift in species composition related to the dispersal ability of Collembola species. Berg et al. (2010) pointed out that dispersal ability must be a highly adaptive trait among animals and plants in the

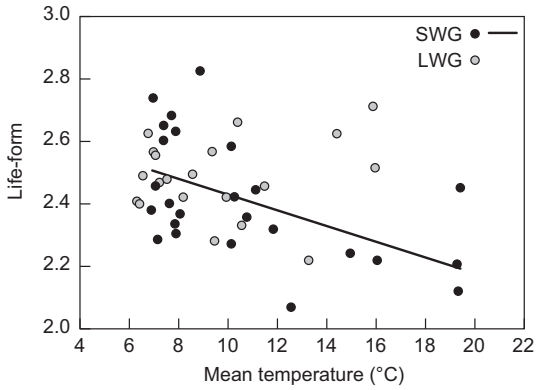

FIGURE 5 Life-form trait (community-weighted mean values) of Collembola at the short-term warming grassland (SWG) and long-term warming grassland (LWG) sites in relation to mean soil temperature. Soil warming had significant effect on life-form at SWG, but not at LWG. Line shows the slope of the linear mixed model. Note that a trait value of three indicates that the community is completely dominated by eu-edaphic species (Table 1). Mean temperature is based on hourly measurements at 10 cm depth during the period from 8 May 2013 until sampling of microarthropods (11 September 2014)

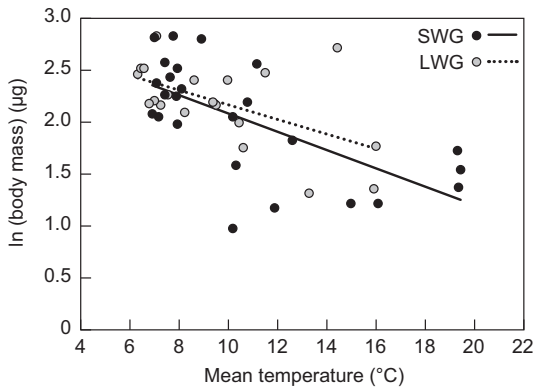

FIGURE 6 Body mass trait (community-weighted mean values) of Collembola at the short-term warming grassland (SWG) and long-term warming grassland (LWG) sites in relation to mean soil temperature. Soil warming had significant effect on body mass at both SWG and LWG. Lines show the slopes of the linear mixed model. Mean temperature is based on hourly measurements at 10 cm depth during the period from 8 May 2013 until sampling of microarthropods (11 September 2014)

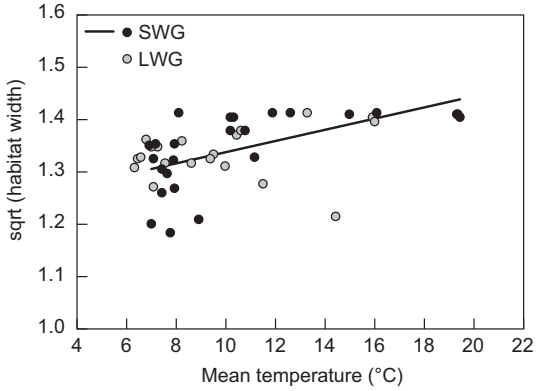

FIGURE 7 Habitat width trait (community-weighted) of Collembola at the short-term warming grassland (SWG) and long-term warming grassland (LWG) sites in relation to mean soil temperature. Soil warming had a significant effect on habitat width at SWG, but not at LWG. Line shows the slope of the linear mixed model. Note that a trait value of 1.41 (sqrt(2)) indicates that the community is completely dominated by eurytopic species (Table 1). Mean temperature is based on hourly measurements at 10 cm depth during the period from 8 May 2013 until sampling of microarthropods (11 September 2014)

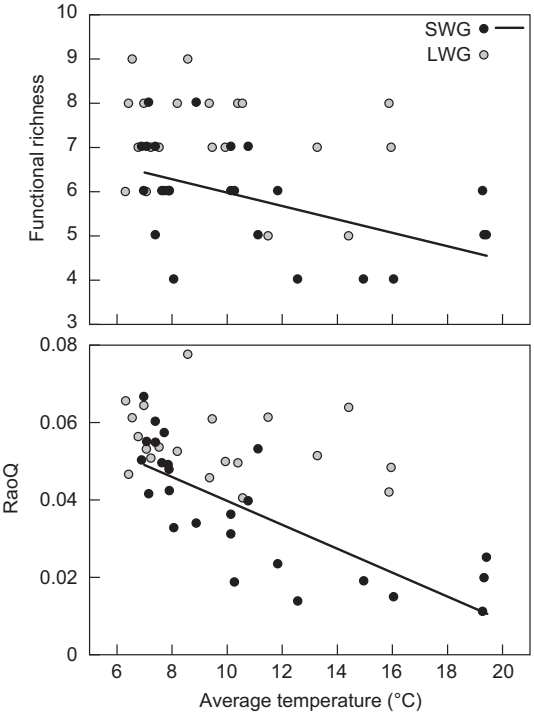

FIGURE 8 The functional richness index (FRic) of the Collembola community (upper panel) and Rao's quadratic entropy index of functional diversity (RaoQ) (lower panel) in relation to mean soil temperature. Soil warming had a significant effect on functional richness and RaoQ at short-term warming grassland (SWG), but not at long-term warming grassland (LWG). Lines show the slopes of the linear mixed model

light of climatic changes, because this would provide an "inexpensive" plastic response to stress imposed by warming: simply move to habitats where conditions are more favourable. Although dispersal ability has been shown to affect Collembola community composition on the long-term, for instance in old fragmented forest landscapes with a patchy distribution of habitat (da Silva et al., 2012), in the short-term, active dispersal may not be of great help for Collembola species, as they are relatively small and live in the pore space of soils. Therefore, Collembola may actively disperse annually only on a centimetre to metre scale (Bengtsson et al., 1994). In a long-term perspective, Collembola may also more depend on passive dispersal, e.g. by wind, rafting on water or by animal transport (Coulson, Hodkinson, Webb, & Harrison, 2002; Hawes, Worland, Convey, & Bale, 2007; Krivolutsky, 2001). Even though Collembola in general do not actively move long distances, the passive dispersal of specimens could provide renewed introduction of species from nearby areas to the warmed soils. This is a possibility since unwarmed areas were adjacent to our study sites.

Interestingly, community-weighted mean habitat width was significantly influenced by temperature at SWG, but not at LWG. The results suggest an initial short-term positive response to warming of eurytopic species at the expense of stenotopic species, but this effect was not seen in the long-term warmed plots. Increased temperature often results in a dryer environment due to increased evaporation from vegetation and soil surface, which can result in a shift in Collembola community composition towards species with a low moisture preference (Makkonen et al., 2011). At the ForHot research site, however, no influence of habitat temperature on moisture preference (as a community-weighted mean trait) of the Collembola community was detected. The lack of response is likely explained by the high annual precipitation (1,400 mm) of south-west Iceland which resulted in relatively high soil water content even at the highest warming levels (Sigurdsson et al., 2016). We therefore conclude that moisture conditions were probably never limiting for Collembola in this habitat (Kærsgaard, Holmstrup, Malte, & Bayley, 2004).

The food preference trait (based on mouthpart morphology) was not sensitive to warming level in our study, which might indicate that food distribution, quality and/or quantity did not become limiting for Collembola along the soil temperature gradients. Most Collembola species are generalist microbivores and shifts in microbial communities, or the vertical stratification of microbes (Berg, Kniese & Verhoef 1998), could therefore have influence on the Collembola community composition (Faber, 1991). A number of studies have shown that increased temperature in general can have impacts on the relative proportions of fungi and bacteria in soil as well as on the microbial biomass (Blankinship et al., 2011; Garcia-Palacios et al., 2015). Studies of bacterial and fungal DNA in soils (5–10 cm depth) of our experimental sites show that the structure of bacterial communities was largely unaffected at temperatures up to 5 and 10°C above normal in SWG and LWG plots respectively (Radujković et al., 2018). This may explain the lack of response in the food preference trait of Collembola if it is assumed that microbial communities in the higher soil layers (0–5 cm) was also not influenced by soil warming.

When evaluating the effects of warming on the categorical traits discussed above, we have to recall that the resolution at which traits were classified was sometimes low, with only a limited number of categories (cf. Table 1), because the traits were derived from species descriptions and field observations. There is therefore a risk that our approach could not detect effects of warming that were in fact there. To improve the use of trait-based methods we need trait measurements that are standardized and based on consensus on how they should be measured, however, such data are currently not available for Collembola (Moretti et al., 2017).

The temperature experienced by ectotherms during ontogenetic development has an impact on adult body size and often results in larger body size at low temperatures and vice versa (Atkinson & Sibly, 1997). This is known as the temperature-size rule, and it has been shown that global warming has already resulted in diminished body size of a number of species (Sheridan & Bickford, 2011). Our study did not address intraspecific phenotypic differences along soil temperature gradients, but focused on body size as a fixed phenotypic trait of species. Doing so, we showed that warming resulted in an increased representation of species of smaller body size. This is in line with metabolic scaling theory showing that metabolic rate scales not only with temperature, but also with body mass, across all animal groups including Collembola (Brown, Gillooly, Allen, Savage, & West, 2004; Meehan, 2006). Moreover, Brown et al. (2004) showed that the universal metabolic scaling rules have the consequence that small species are favoured at high temperature because small species have higher developmental rates and higher maximal rates of population growth than species of larger body size. In a warmer environment, one would therefore expect a shift towards smaller species, and indeed this is what we observed in both SWG and LWG. If we assume that other soil animals will also tend to be smaller when temperature increases, the potential consequences may be that turnover and growth of soil fauna in general will increase and strengthen their role in decomposition processes.

We hypothesized that epigeic and hemi-edaphic species would have an advantage as compared to eu-edaphic species when the temperature increases (Bokhorst et al., 2012; Van Straalen, 1994). Due to the method of sampling we have no reliable estimates of the abundance of epigeic species. However, it seemed that the hemi-edaphic species increased their abundance with warming in the short-term (SWG), whereas eu-edaphic species as a whole were either unresponsive or slightly negatively influenced by warming (although this trend was only marginally significant). Interestingly, the abundance of hemi-edaphic species as a group decreased when warming had lasted for decades or centuries (LWG). This suggests that conditions have changed in the fragmentation layer (where the hemi-edaphic species primarily reside) as a result of long-term warming, for example a decrease in the quality of organic matter. Other measurements at our study sites have shown that warming (even modest soil warming levels of 1 to 3°C) has caused a substantial loss of soil organic matter in both SWG and LWG sites (Leblans, 2016; Poeplau, Kätterer, Leblans, & Sigurdsson, 2017). This loss was mainly due to enhanced decomposition accompanied by a decrease in the quality of organic matter as celluloses disappear and material becomes enriched with chemical recalcitrant components. Such changes may negatively affect microbial biomass and activity and Collembola abundance (Berg, Kniese, Bedaux, et al., 1998; Berg, Kniese, Verhoef, 1998). These changes in quality are much faster in fragmented litter than in humus (where the eu-edaphic species primarily reside) which may also explain why hemi-edaphic, but not eu-edaphic species were affected by warming. These explanations remain speculative, however, since we have no suitable data to support them in this particular case study.

As judged from the functional diversity indices (FRic and RaoQ), despite a drop in functional diversity in the short-term, the Collembola community displayed a considerable resilience towards warming in the long-term. This is remarkable since the change in temperature was almost 10°C (almost triple the current mean T_s of unwarmed areas), and much higher than other field studies have applied (Blankinship et al., 2011). Perhaps contradictory to these results, we observed a reduction in taxonomic diversity (species richness) with warming in both SWG and LWG. However, the decrease in species richness was modest (*c.* 10% lower than at control temperature) compared to the substantial decrease in functional diversity.

Two mechanisms may have played a role in the small difference between Collembola communities along the thermal gradient in the LWG plots. First, species that were lost in the warmed soils may have been replaced by more tolerant species having the same ecological traits. For example abundance of the hemi-edaphic species *Folsomia quadrioculata* decreased with temperature in LWG, whereas *Sphaeridia pumilis* (with almost the same multiple-trait combination) had the highest abundance in warmed plots (Table S4). Second, natural selection favouring the individuals with highest fitness under the warmer conditions may have led to evolutionary adaptation of species (Hoffmann & Parsons, 1991). Alternatively, phenotypic plasticity may drive convergence of trait values in communities under higher temperatures (Le Lann et al., 2014), which may be mitigated in the longer term by divergent selection on species. In our study, two eu-edaphic species (*Protaphorura pseudovanderdrifti* and *Isotomiella minor*) were negatively influenced by warming in SWG, whereas this effect was absent or alleviated in LWG suggesting that genetic adaptation could have occurred over a longer time period. Our ongoing laboratory studies on the former of these species may provide an answer to this question. It has been shown in similar climate change studies that microevolutionary responses can take place rather quickly, i.e. over a few years and relatively few generations (Bataillon et al., 2016; Van Doorslaer, Stoks, Jeppesen, & De Meester, 2007). If rapid evolutionary responses are common and applicable to other species, such responses should be included when predicting species distributions based on current climate change projections. Our present field study suggests that evolutionary processes do play a part in the observed differences in the Collembola communities when comparing short-term and long-term scenarios, but this should be confirmed with experimental evidence.

Although the Collembola community was apparently only temporarily affected by substantial warming, long-term climate change can have drastic effects on functionality of the soil. Hence, the apparent resilience of Collembola functional diversity, which is only

one aspect of the ecosystem, should not lead us to conclude that overall soil functionality will not be affected in the most likely future climate change scenario, but it shows that soil fauna communities can have considerable potential for adjusting to climate change.

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AUTHORS' CONTRIBUTIONS

B.D.S., N.I.W.L., B.K.E., J.E., M.P.B., K.I.-M. and M.H. conceived the ideas and designed methodology; M.H., S.S. and N.I.W.L. collected the data; B.K.E., J.E., M.P.B. and M.H. analysed the data; M.H., M.P.B. and B.K.E. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The authors declare no conflicts of interest.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository: https://doi.org/10.5061/dryad.21fm7 (Holmstrup et al., 2018).

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SUPPORTING INFORMATION

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